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Phylogenetic Studies of the Subgenus *Nialoe* (s. lat.) (Coleoptera, Carabidae, Genus *Pterostichus*), Part 1: Homology of the Component Parts of Male Genitalia and Higher Phylogeny

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ABSTRACT—A phylogenetic hypothesis of the subgenus *Nialoe* (s. lat.) of genus *Pterostichus* is proposed based on a cladistic analysis of seventeen morphological characters. Through comparative studies of the sclerites on the endophallus of male genitalia, it became apparent that the arrangement of these sclerites reflects seven different origins. The results show that *Nialoe* (s. lat.) is monophyletic and composed of four clades, while some traditional taxa are para- or polyphyletic, and are defined only by symplesiomorphies. *Pterostichus* (*Nialoe*) *mosaicus* sp. nov., which is indispensable for tracing the homology of sclerites in this subgenus, is described.

Key wards: *Nialoe* (s. lat.), sclerite, homology, phylogeny, new species

INTRODUCTION

The subgenus *Nialoe* Tanaka, 1958 is one of the more diverse subgenera of the genus *Pterostichus* Bonelli, 1810, and is characterized by the sexual morphology of male sternum 7 in most species. This subgenus is apterous, and its distribution is primarily the Sea of Japan region of the Far East (Jedlička, 1962; Tanaka, 1985; Kasahara, 1988; Kryzhanovskij *et al.*, 1995; Park and Paik, 2001; Bousquet, 2003). The subgenus includes approximately 120 species that have either been united into one subgenus (*Lianoe*: Jedlička, 1962; *Nialoe*: Habu, 1981; *Pterostichus*: Tanaka, 1985), or separated into several subgenera (Kasahara, 1988; Park and Paik, 2001; Bousquet, 2003).

Nialoe was originally erected by Tanaka (1958) for *Pterostichus asymmetricus* Bates, 1883 as a subgenus related to *Lianoe* Gozis, 1882 of the Pyrénées. Tanaka (1958) included in the subgenus species that have an aedeagus similar in shape to that of *P. asymmetricus*. Around the same time, Ishida (1958) established *Paralianoe* for *P. uenoi*, and included its allies in that subgenus. Later, Nakane (1979) proposed *Epinialoe* for *P. spiculifer*. In the same paper, Nakane and Straneo described a new subgenus, *Daisenialoe*, to accommodate *P. fujimurai*, which has some peculiarities in its external structures. Kasahara and Ito (1987) described *Sphodroferonia*, with its type species *P. miyamai*, emphasizing its external peculiarities. Park and Kwon (1996) described *Koreanialoe* from South Korea, with its type species *P. teretis*, and Berlov and Plutenko (1997) erected *Natalianoe* for *P. microps* of Wladiwstok, Russia, which had formerly been referred to *Paralianoe* (Kryzhanovskij *et al.*, 1995).

Thus, seven subgenera have been proposed to contain the 120 species first grouped into the subgenus *Nialoe*. However, their phylogenetic relationships have never been established on the basis of reliable evidence, and there is considerable incongruence among classifications by different authors. Jedlička (1962) included all *Nialoe* species in *Lianoe*. Habu (1981) criticized the superfluous split of subgenera, and treated them all as one subgenus, *Nialoe*. Tanaka (1985) ignored the subgenera erected for the Japanese species and regarded them all as members of the subgenus *Pterostichus* (s. lat.). Later, Kasahara (1988) divided 65 species into eight groups based on external structures (sexual characteristics of male sternum 7; number of setae on antennal segment 2) and parts of the male genitalia (right paramere; some of the sclerites on the endophallus). However, he did not discuss the phylogenetic relationships among the eight groups.

Taxonomic problems arose in this group partly because no researchers had used male endophallic structures, which are known to be useful phylogenetic characteristics in the Pterostichini (Allen, 1980; Koch, 1986; Nemoto, 1988, 1989a, b; Brandmayr and Brandmayr, 1994; Bousquet, 1999; Sasakawa, 2004, 2005a, b; Sasakawa and Kubota, 2005). In some *Nialoe* species, the presence of sclerites on the surface of the endophallus was known (Tanaka, 1961; Nemoto,

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1988, 1989a; Park and Kwon, 1996; Morita and Kanie, 1997; Morita, 1996a, 1998, 2001; Lafer *et al.*, 2001; Sugimura, 2002); however, authors used them as diagnostic characters only in particular groups (Tanaka, 1961; Kasahara, 1988; Park and Kwon, 1996; Morita, 1998), rather than examining their homologies among taxa.

The main purpose of the present study was to elucidate the phylogeny of the subgenus *Nialoe* (s. lat.). First, I describe a new species that has proven to be useful in tracing the homology of endophallic sclerites. Second, I review the homology of the component parts of the male genitalia, primarily the sclerites on the surface of the endophallus. Third, I propose a phylogenetic hypothesis of *Nialoe* (s. lat.) using cladistic methods and based on seventeen morphological characters (10 male genitalia, 1 female genitalia, 6 external structures).

MATERIALS AND METHODS

Most of the specimens used in the present study were from the author's collection. The rest of the material was loaned from the following public or private collections: Laboratory of Forest Zoology, Department of Forest Science, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan (FZUT); The National Science Museum, Tokyo, Japan (NSMT); National Institute for Agro-Environmental Sciences, Tsukuba, Japan (NIAES) and the collection of Mr. K. Akita (Mie, Japan), Mr. H. Karube (Kanagawa Prefectural Museum of Natural History, Kanagawa, Japan), and Mr. K. Matsumoto (Kagawa, Japan). Most of the type species of subgenera are included in these collection's, and were examined directly. Taxonomic information on two indispensable specimens, male *P. teretis* (type species of *Koreanialoe*; female is unknown) and female *P. microps* (type species of *Natalianoe*), was obtained from the peer-reviewed literature (Jedlička, 1962; Park and Kwon, 1996; Berlov and Plutenko, 1997). Morphological characters not referred to in the literature were coded as missing. Four species, *P.* (*Pterostichus* s. str.) *cristatus* (Dufour), *P.* (*Lianoe*) *dufouri* (Dejean), *P.* (*Myosodus*) *schonherri* Faldermann, and *P.* (*M.*) *lacunosus roubalianus* (Lutshnik), were used for outgroup comparison. Dissection techniques and the terminology for female genitalia follow Bousquet (1999), but new terminology is proposed here in for most other characters.

Seventeen characters (10 male genitalia, 1 female genitalia and 6 external structures) were observed from adults of 30 species, and all characters were treated as unordered (Appendix 1). Phylogenetic analyses were performed by PAUP* ver. 4.0 (Swofford, 2002) with a heuristic search. The analyses began from 10 replicates of random trees, with TBR branch swapping performed using both equal and successive character weighting (Farris, 1969). In successive weighting, each character was weighted by the rescaled consistency index (RC), but tree lengths, the consistency index (CI), and the retention index (RI) for the resultant trees were calculated with equally weighted characters. Statistical support for nodes was evaluated using a bootstrap probability calculated from 100 replicates. Character changes were reconstructed using ACCTRAN optimization.

My series of taxonomic studies of this group treats all species under the subgenus *Nialoe* (s. lat., *i.e.*, the subgenus *Nialoe sensu* Habu, 1981; Nemoto, 1988, 1989a), for the following reasons. First, it is not always possible to examine all species directly (including type species); therefore, the phylogenetic relationships proposed may change subtly in future analyses. Second, it is important to enhance our understanding of the phylogenetic relationships of this group, rather than to adhere strictly to a formal taxonomy.

SYSTEMATIC ACCOUNT

Subgenus *Nialoe* Tanaka, 1958

Nialoe Tanaka, 1958: 82. Type species: *Pterostichus asymmetricus* Bates, 1883

Nialoe as treated here includes East Asian species which Jedlička (1962) treated as *Lianoe*; Habu (1981) as *Nialoe*; and Kasahara (1988) as *Pterostichus* (s. lat.). In the present study, the presence of setae on the ventral side of the last tarsal segment provides support for monophyly of this subgenus (see phylogenetic section). The species which I examined share the following character states.

Description. [External structures]: Body medium to large (minimum, 9.5mm: *P.* (*N.*) *ohkurai* Morita, [Morita, 1996b]; maximum, 24mm: *P.* (*N.*) *ishikawai* Nemoto [Nemoto, 1988]). Dorsal surface of body black and opaque to shiny without metallic luster. Legs reddish-brown to black. Head normal to large; antennal segment 3 without pubescence except for *P. fujimurai* and *P. shotaroi*. Pronotum cordate to almost square, with single laterobasal impression on each side. Elytra long-oval; intervals not interrupted. Male sternum 7 with sexual characteristic in most species. [Male genitalia]: Aedeagus robust; right paramere short to elongated; left one square. Endophallus large, with vent toward left lateroventral to ventral direction, except for *P. opacipennis* and its allies with short, straight endophallus; gonopore weakly sclerotized with gonoporal piece. [Female genitalia]: Median oviduct connected to seminal canal just anterior to the vagina; apophyses of basal part of median oviduct and seminal canal weakly to distinctly sclerotized; receptaculum almost straight to strongly bent.

Pterostichus (*Nialoe*) *mosaicus* sp. nov. (Fig. 1)

This species is unique in having a mosaic combination of external structures of some Korean and Japanese species. The sexual condition of male sternum 7 is considered as an apomorphic character state also possessed by *P. touzalini* and its allies of the Korea Peninsula and the adjacent islands. On the other hand, the opaque female elytra are considered as an apomorphic state shown in common with some species of the *P. sphodroformis* group of Japan (Kasahara, 1988). However, the endophallus of this species is a combination of presumed plesiomorphic character states, whereby it is possible to trace homologies between some Korean and Japanese species (Figs. 2–4).

Diagnosis. This species is similar to *P.* (*N.*) *gotoensis* Kasahara and Matsumoto, 1990 externally, but easily distinguished from the latter by the shape of the aedeagus and the prominence on male sternum 7.

Description. [External structures]: Length: ♂, 18.8–18.9 mm (n=2), ♀, 19.4 mm (n=1). Dorsal surface of body black and shiny, except for female elytra which are opaque. Legs reddish-brown. Head normal. Pronotum cordate; surface smooth except for laterobasal impressions which are slightly

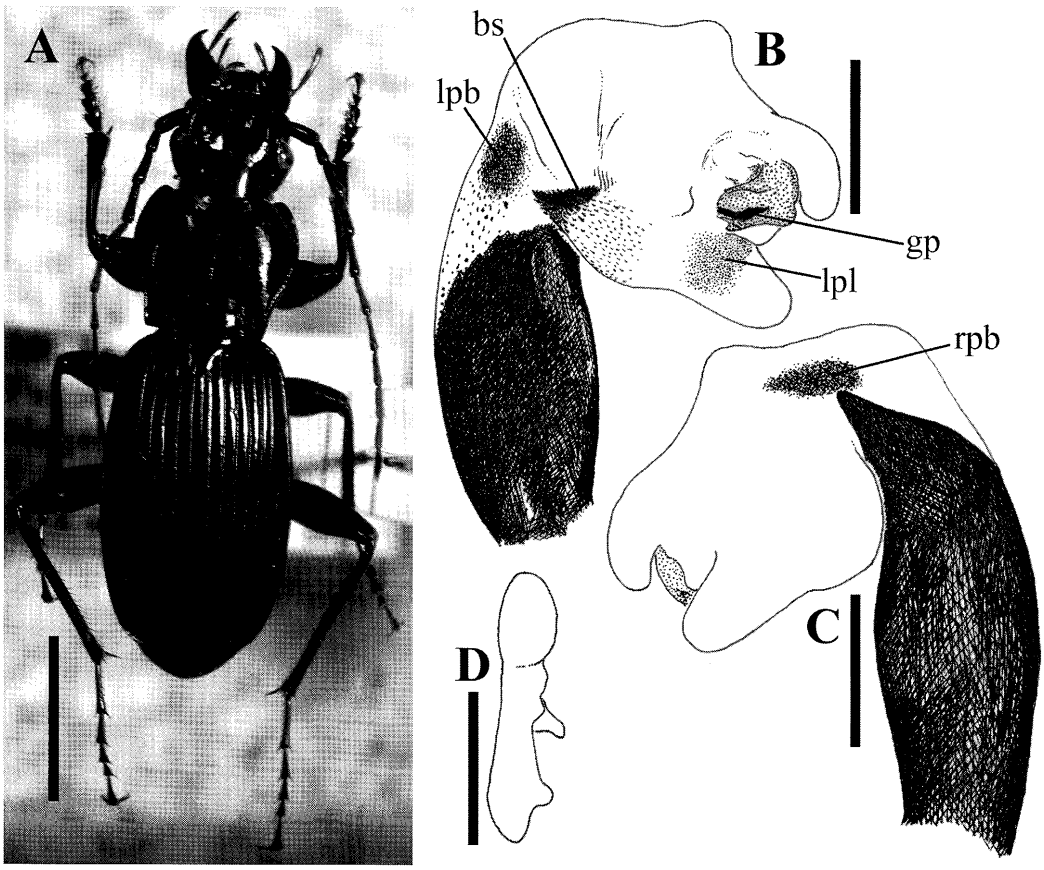

Fig. 1. *Pterostichus* (*Nialoe*) *mosaicus* sp. nov. (A) Dorsal view. (B) Dorsal view of endophallus. (C) Ventral view of endophallus. (D) Right lateral view of right paramere. gp, gonoporal piece; rpb, right pigmented band; lpb, left pigmented band; bs, basal sclerite; lpl, left preapical lobe. Scale lines: 5 mm for (A); 1 mm for (B–D). The basal part of the aedeagus is omitted.

punctate. Elytra long-oval; three dorsal pores on interval 3. Ventral side almost smooth; submentum with a pair of setae. Male sternum 7 with apical prominence; prominence broad and trapezoidal; prominence narrower posteriorly than anteriorly; surface of prominence shallowly cup-shaped from the ventral view. [Male genitalia]: Aedeagus without a distinct tubercle, and shallowly dished on the left ventral side near ostium. Endophallus large, moderately bent in left ventral direction; pigmented bands present on both lateral sides near ostium; sclerotization of the bands weak; basal sclerite distinct, with swelling more on the dorsal side; right surface of endophallus swollen; small but distinct swelling present on dorsal surface near gonopore; weakly hooked lobe present on right ventral side near ostium; distinct lobe present on left side near ostium; apical lobe weakly but distinctly sclerotized; gonopore weakly sclerotized, with gonoporal piece. Right paramere short and rounded apically. Left paramere square. [Female genitalia]: Vagina with slightly sclerotized part around median oviduct; surface without conspicuous pigmentation; apophyses of median oviduct and seminal canal weakly sclerotized over their entirety.

Locality. Fukuejima Is., Gotô Isls., Nagasaki, Japan.

Holotype. ♂, Mt. Sasadake, Fukuejima Is., Gotô Isls., Nagasaki, Japan; 1. x. 1996, (H. Karube), in NSMT collection.

Paratypes. 1 ♂1 ♀, same data as holotype, in NSMT collection.

Other specimens examined. Pterostichus gotoensis Kasahara and Matsumoto: 1 ♂, Wakamatsu-goe, Wakamatsujima Is., Gotô Isls., Nagasaki, Japan, 1. v. 1988, (T. Matsumoto), holotype, (NSMT) (endophallus not everted); 1♀, ditto, 18. viii. 1992, (K. Matsumoto), (NSMT).

Notes. Shape of spermatheca could not be observed because of damage during dissection.

HOMOLOGY OF THE COMPONENT PARTS OF THE MALE GENITALIA

In the present study, seven sclerites of different origins are recognized on the endophallus, the homology of which are considered as follows.

Right pigmented band (rpb in Figs. 1, 2; character 2 in Appendix 2)

In some *Nialoe* species (*e.g.*, *P.* (*N.*) *mosaicus*), there is a pigmented band on the right laterodorsal surface of the membranous part near the ostium. The pigmentation varies from rudimentary to distinct at the subspecific level.

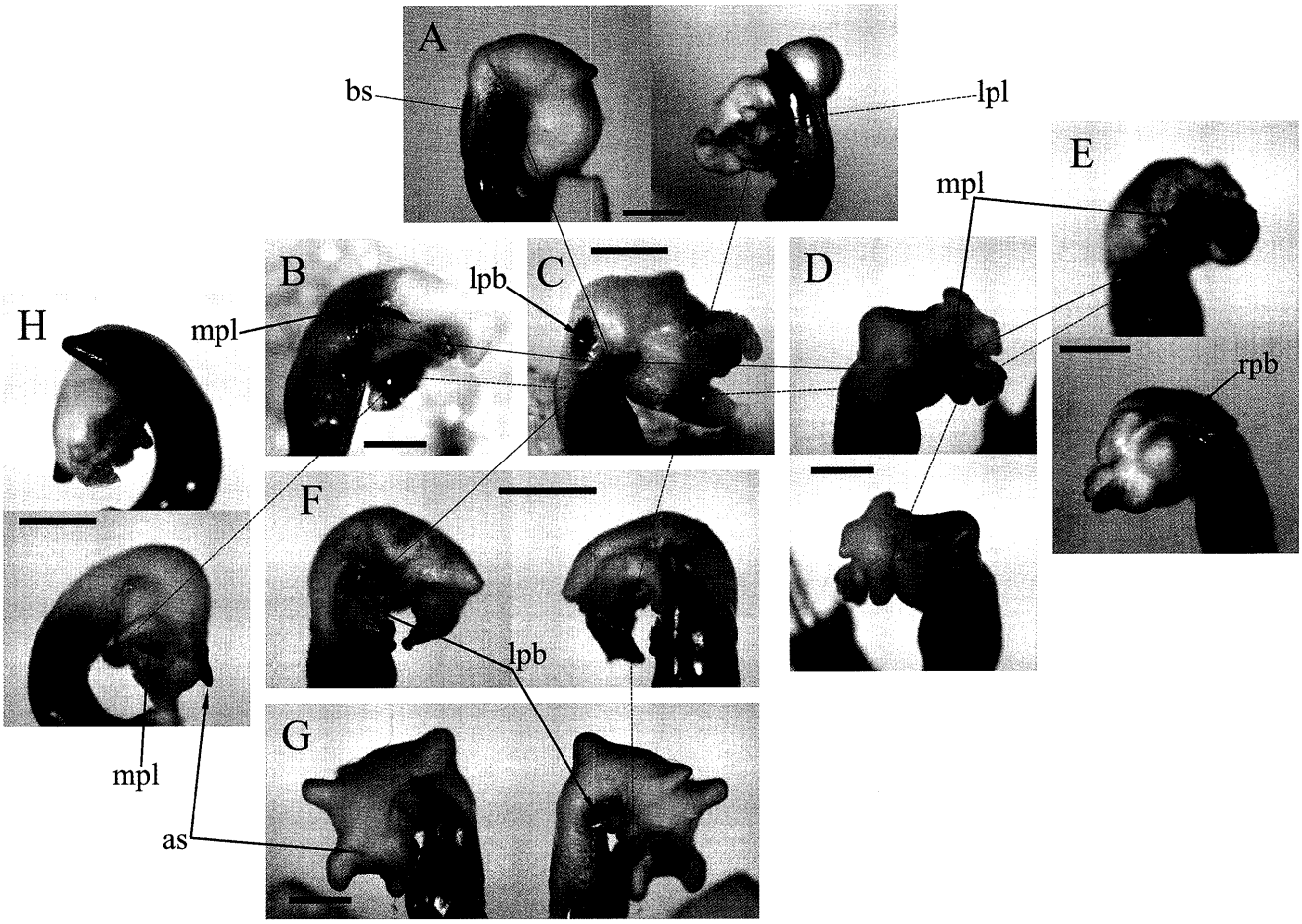

Fig. 2. Homology of sclerites on the endophallus. (A) *Pterostichus* (*Nialoe*) *ishizuchiensis*. (B) *P.* (*N.*) *symmetricus*. (C) *P.* (*N.*) *mosaicus*. (D) *P.* (*N.*) *mucronatus*. (E) *P.* (*N.*) *abaciformis*. (F) *P.* (*N.*) *dandonis*. (G) *P.* (*N.*) *katashinensis naganoensis*. (H) *P.* (*Lianoe*) *dufouri*. rpb, right pigmented band; lpb, left pigmented band; bs, basal sclerite; mpl, median pigmented lobe; lpl, left preapical lobe; as, apical sclerite. Solid lines refer to homology of the basal sclerotization (bs), and dotted ones to that of the left preapical lobe. Indications of the gonoporal piece are omitted because of their obvious homology. Scale lines: 1 mm.

Left pigmented band (lpb in Figs. 1–4; character 3 in Appendix 2)

There is a pigmented band on the left latero- to laterodorsal surface of the membranous part near the ostium. The pigmentation varies from rudimentary to distinct at the subspecific level. In *P.* (*N.*) *spiculifer* and its allies (= *Epinialoe* Nakane, 1979 *sensu* Kasahara, 1988), the posterior end of the pigmented band is connected to the anterior end of the basal sclerite. This character is synonymous with "poorly sclerotized plate" *sensu* Morita and Kanie, 1997. However, their observation was based on specimens where the endophallus was not everted (Morita and Kanie, 1997: 166, Fig. 3), so that only the basal part of this band was observed. Therefore, "plate" is an inappropriate term for this character.

Basal sclerite (bs in Figs. 1–4; character 4 in Appendix 2)

There is a sclerite on the left laterodorsal to lateral surface of the membranous part near the ostium. Its shape and degree of sclerotization vary at the subspecific level. This character is synonymous with "apical sclerite" *sensu* Tanaka, 1961, "median macula" *sensu* Nemoto, 1989a, part of the "pigmented pad" *sensu* Nemoto, 1989a, and "apical copulatory piece" *sensu* Morita, 1998. In Tanaka's (1961) study, the endophallus was not everted, so references to "apical" and "basal" in the position of these sclerites are reversed. Nemoto (1989a) named this character "median macula". However, most species have the sclerite at the basal part of the endophallus, so that "median" is unique in *P.* (*N.*) *plesiomorphus*, with which Nemoto (1989a) defined this structure's terminology (Nemoto, 1989a: 3, Fig. 3). In the same paper, Nemoto (1989a) considered the "median macula" (basal sclerite in the present study) of *P.* (*N.*) *mucronatus* and *P.* (*N.*) *shiibanus* to be a "pigmented pad" (left preapical lobe in the present study; Nemoto 1989a: 4, Figs. 9–12). These two species do have one sclerite on the left lateral side on the endophallus; however, the positions of the sclerites are not correctly shown in Nemoto's (1989a) illustrations because the endophallus was not fully everted. I examined the completely everted endophallus of *P.* (*N.*) *mucronatus* and *P.* (*N.*) *ishizuchiensis* (probably a local race of *P.* (*N.*) *shiibanus*), and confirmed that these species have

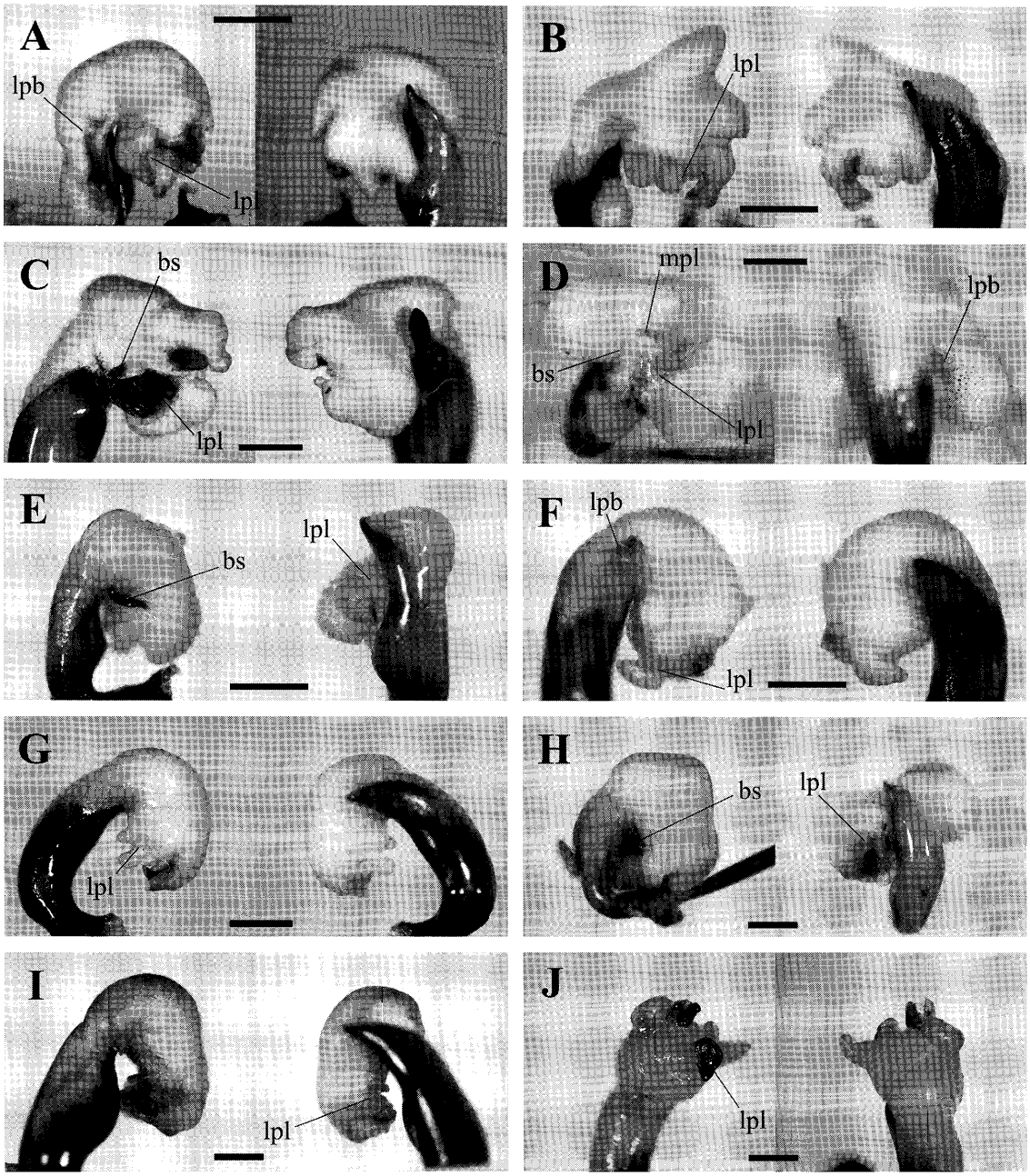

Fig. 3. Endophalli of *Nialoe* (s. lat.) (right lateral view, left lateral view). (A) *Pterostichus* (*Nialoe*) *fujimurai*. (B) *P.* (*N.*) *mirificus*. (C) *P.* (*N.*) *yakushimanus*. (D) *P.* (*N.*) *plesiomorphus*. (E) *P.* (*N.*) *miyamai*. (F) *P.* (*N.*) *macrogenys*. (G) *P. microps*. (H) *P.* (*N.*) *yoshidai*. (I) *P.* (*N.*) *bellator*. (J) *P.* (*N.*) *opacipennis*. rpb, right pigmented band; lpb, left pigmented band; bs, basal sclerite; mpl, median pigmented lobe; lpl, left preapical lobe. Indications of the gonoporal piece are omitted because of their obvious homology. Scale lines: 1 mm.

the sclerite that Nemoto (1989a) termed the "pigmented pad" (left preapical lobe in the present study), but at a more basal position on the endophallus than in his illustration. Thus, because Nemoto (1989a) misidentified the homology among the sclerites, the "median macula" *sensu* Nemoto, 1989a is not always "macula". Morita (1998) illustrated this character of *P.* (*N.*) *abaciformis* and its allied species and named it "apical copulatory piece". However, as with Tanaka's (1961) study, "apical" is an inappropriate term for this character.

Median pigmented lobe (mpl in Figs. 2, 4; character 5 in Appendix 2)

There is a weakly to strongly pigmented lobe on the middle dorsal surface of the endophallus in some *Nialoe* species (*e.g.*, *P.* (*N.*) *symmetricus*) and outgroup species (*P.* (*Lianoe*) *dufouri* and *P.* (*Pterostichus* s. str.) *cristatus*). This character is a synonym of "median lobe" *sensu* Nemoto, 1989a. The definition of this character is exactly the same as that of "median lobe" in Nemoto (1989a; in *P.* (*N.*) *mucronatus*; however, it was overlooked, presumably because of

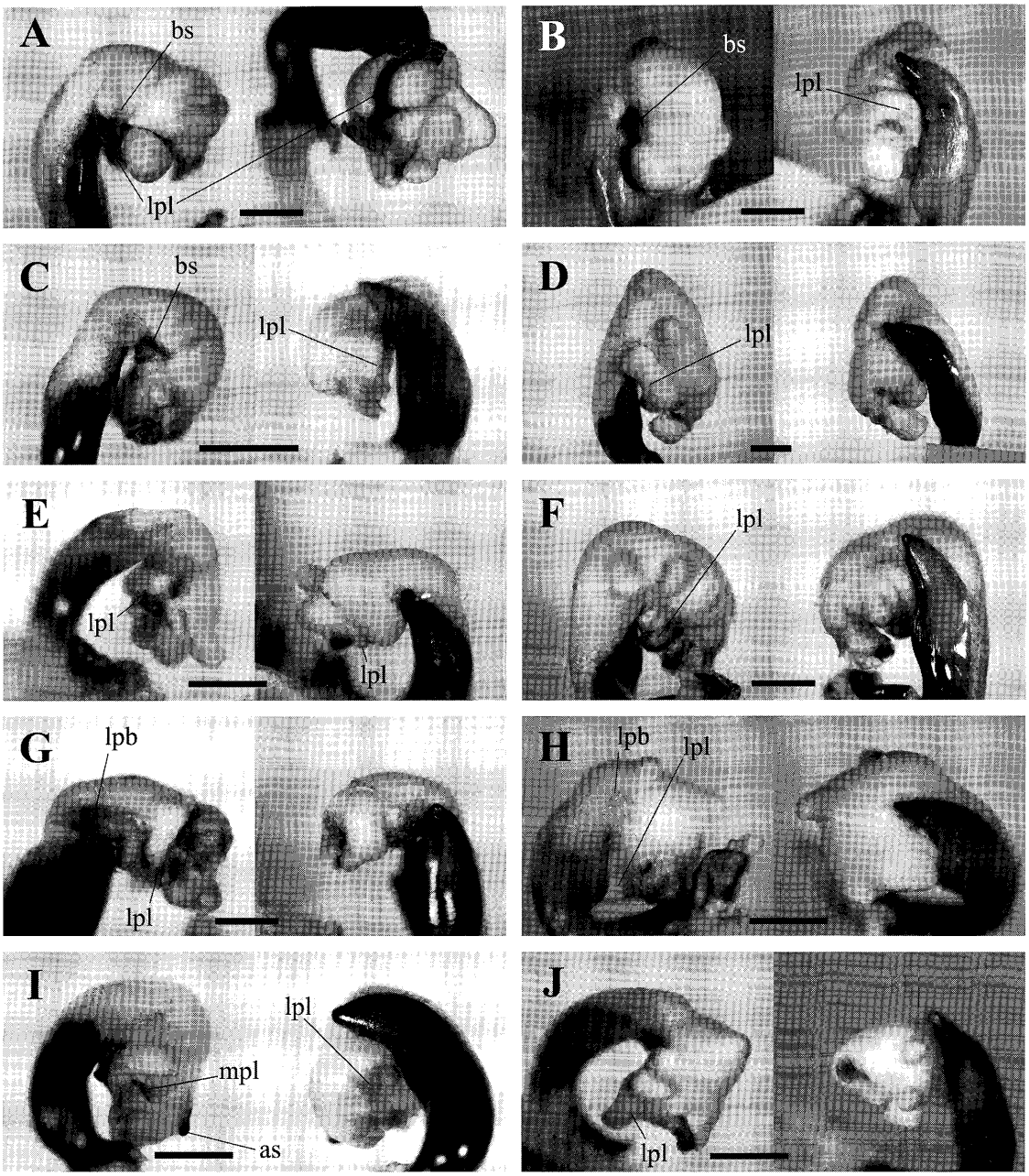

Fig. 4. Endophalli of *Nialoe* (s. lat.), *Pterostichus* (s. str.) and *Myosodus* (right lateral view, left lateral view). (A) *Pterostichus* (*Nialoe*) *macrocephalus*. (B) *P.* (*N.*) *sphodroformis*. (C) *P.* (*N.*) *mashidai*. (D) *P.* (*N.*) *sincerus*. (E) *P.* (*N.*) *praedo*. (F) *P.* (*N.*) *uenoi*. (G) *P.* (*N.*) *omogoensis*. (H) *P.* (*N.*) *latistylis*. (I) *P.* (*Pterostichus* s. str.) *cristatus*. (J) *P.* (*Myosodus*) *lacunosus roubalianus*. rpb, right pigmented band; lpb, left pigmented band; bs, basal sclerite; mpl, media pigmented lobe; lpl, left preapical lobe; as, apical sclerite. Indications of the gonoporal piece are omitted because of its obvious homology. Scale lines: 1 mm.

insufficient eversion of the endophallus [p4, Fig. 11]). In the present study, I propose the term median pigmented lobe for this character, because the term "median lobe" means aedeagus or penis in the general terminology of the Coleoptera.

Left preapical lobe (lpl in Figs. 1–4; characters 6 and 7 in Appendix 2)

In most *Nialoe* species, the dorsal surface of the left preapical lobe is more-or-less sclerotized. In some species, it is distinctly sclerotized and concave (*e.g.*, *P.* (*N.*) *symmetricus*). By tracing homologies among species, it is revealed that this character is a specialized form of the left preapical lobe (Fig. 2). This character is synonymous with "lobe α" *sensu* Nemoto, 1988, part of the "pigmented pad" *sensu* Nemoto, 1989a, and "apical copulatory piece" *sensu* Morita, 2001.

Gonoporal piece (gp in Fig. 1; character 8 in Appendix 2)

All species of *Nialoe* have a weakly sclerotized gonop-

ore, of which the dorsal aspect is strongly sclerotized. Many authors have described the dorsal scletotized portion as a "copulatory piece" or used an analogous term ("apical sclerite" [Tanaka, 1961], "copulatory piece" [Morita, 2003] "proximal copulatory piece" [Morita, 2001]). Only Nemoto (1988, 1989a) distinguished it from other sclerites on the endophallus, and named it the gonoporal piece. In the present study, I adopt Nemoto's (1988, 1989a) term for this character.

Apical sclerite (as in Figs. 2, 4; character 9 in Appendix 2)

In some *Nialoe* species (*e.g.*, *P.* (*N.*) *katashinensis naganoensis*), the ventral surface of the endophallus near the gonopore is rudimentarily pigmented. Some outgroup species (*P.* (*Lianoe*) *dufouri* and *P.* (*Pterostichus* s. str.) *cristatus*) have a large sclerotized projection in the corresponding spot, so I propose the term apical sclerite to represent this character. No other authors have described this character.

PHYLOGENY AND CHARACTER EVOLUTION

From the equal-weighting analysis, 20 trees of 70 steps were obtained, with CI=0.586 and RI=0.729. The strict consensus tree was well resolved at the species level, except for Lineage A (defined below), where monophyly and some internal nodes were not supported. The monophyly of *Nialoe* was not recovered in the consensus tree (Fig. 5).

From the successive-weighting analysis, five trees were obtained. Their tree lengths, CI, and RI were equal to those of the equal-weighting analysis. Tree resolution was better, and four lineages were emerged (Fig. 5, 6). The monophyly of the *Pterostichus* (s. str.) + *Lianoe* + *Nialoe* (s. lat.) lineage was supported by a moderate bootstrap value (78%). Although the bootstrap support is relatively low (57%), the monophyly of *Nialoe* (s. lat.) was supported by the absence of setae on the ventral side of the last tarsal segment (character 14). This character state is a synapomorphy of *Nialoe*.

Lineage A comprises the species that Kasahara (1988) referred to as the *mirificus*, *fujimurai*, *asymmetricus*, *spiculifer*, and *uenoi* groups. The shape of the endophallus (character 10) and the presence of setae on antennal segment 2 (character 12) support the monophyly of this lineage. Lineage B includes *P.* (*N.*) *macrogenys*, *P.* (*N.*) *ballator*, *P.* (*N.*) *opacipennis*, and *P.* (*N.*) *teretis*, and its monophyly is supported by pigmentation of the innermost part of the ventral side of the vagina (character 11). Lineage C comprises *P.* (*N.*) *microps*, *P.* (*N.*) *praedo* and *P.* (*N.*) *sincerus*. The monophyly of this lineage is supported by the opaque dorsal surface of the pronotum and elytra (character 13). The remaining species are included in Lineage D, monophyly of which is supported by the presence of the basal sclerite (character 4). In all lineages (A–D), monophyly and most of the species

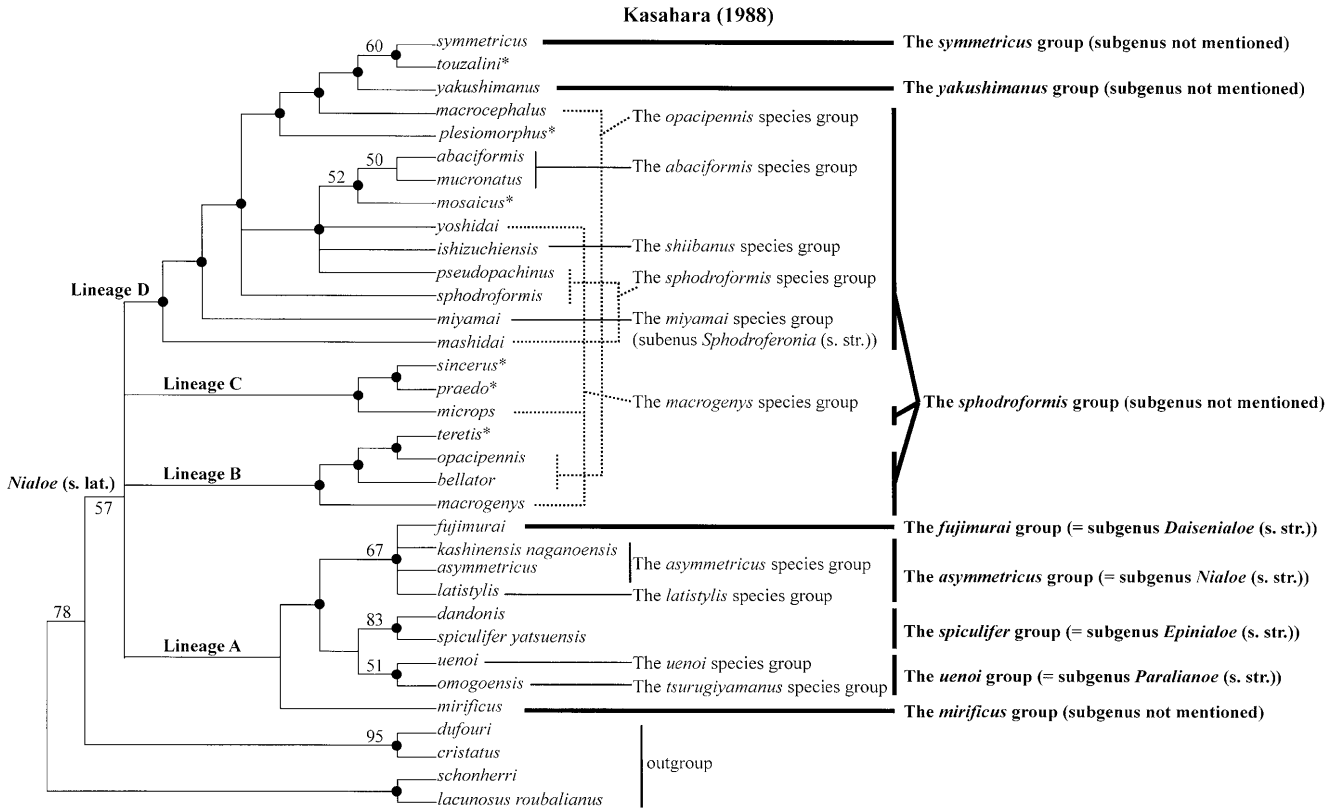

Fig. 5. Strict consensus tree of the 5 trees obtained by the succesive-weighting method. Closed circles indicate nodes shared by the consensus trees of the 20 trees resulting from the equal-weighting analysis. The taxonomy from Kasahara (1988) is represented for comparison. Species with an asterisk are not included in Kasahara's (1988) study.

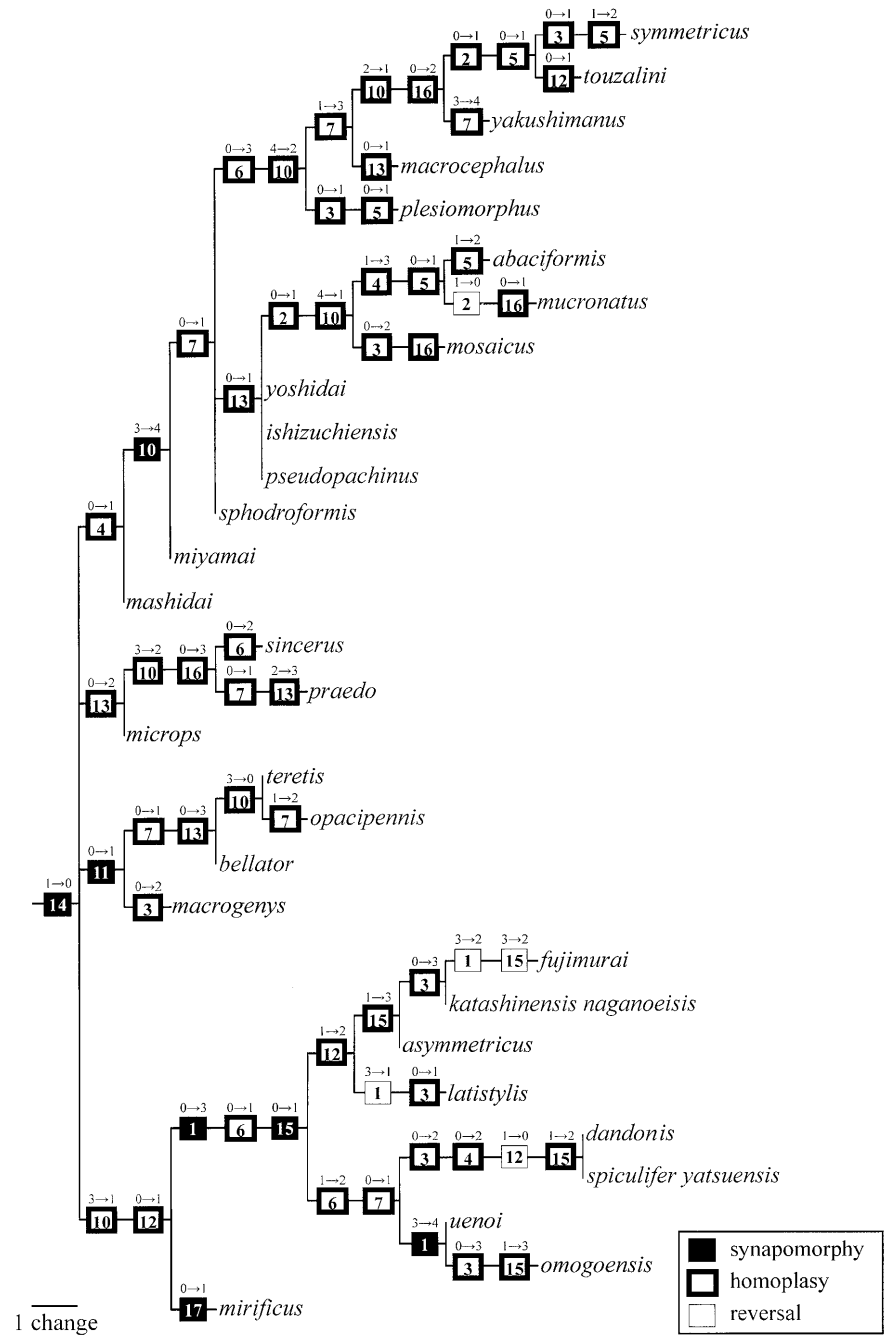

Fig. 6. Phylogeny and possible character evolution of *Nialoe* (s. lat.) based on one of most parsimonious trees obtained by the succesive-weighting method. Numbers in the squares indicate characters in Appendix 2, and numbers above the squares indicate changes in character states. Character-state changes were reconstructed with ACCTRAN optimization.

relationships were not supported by high bootstrap values.

DISCUSSION

This study provides for the first time a phylogenetic hypothesis of *Nialoe*, based on the cladistic analysis of 17 morphological characters. It became apparent that endophallic structures are well developed and diverged within *Nialoe*, and that they can contribute significantly to the reconstruction of the phylogeny of this group. The phylogeny of *Nialoe* was fully resolved, except for relationships among the four largest clades (Lineages A–D). The trees obtained here suggest that some traditional taxa are not monophyletic.

In Lineage A, monophyly of each of the groups proposed by Kasahara (1988) is supported, except for the *asymmetricus* group. The *asymmetricus* group is paraphyletic in all trees obtained, because the *fujimurai* group consistently occupies the most derived branch of the *asymmetricus* group + *fujimurai* group lineage. The characters that

Kasahara (1988) regarded as diagnostic of the *asymmetricus* group, (sexual characteristics of male sternum 7, more than three setae on antennal segment 2, tubercle on the right ventral surface of the aedeagus, and a short to elongate right paramere) are also present in the *fujimurai* group. In other words, these are symplesiomorphies of the *asymmetricus* group + *fujimurai* group lineage.

In Lineages B–D, monophyly of some species groups of the *sphodroformis* group was not supported (Fig. 5). As stated by Kasahara (1988), the *sphodroformis* group is less specialized externally, except for the two macrocephalic species groups (the *opacipennis* and *macrogenys* species groups); therefore, their taxonomy has been based only on the "similarity" of the external characters.

The two macrocephalic species groups are both split within Lineages B–D (*opacipennis* species group: *P.* (*N.*) *opacipennis* and *P.* (*N.*) *bellator* are in Lineage B, *P.* (*N.*) *macrocephalus* in Lineage D; *macrogenys* species group: *P.* (*N.*) *macrogenys* is in Lineage B, *P.* (*N.*) *microps* in Lineage C, and *P.* (*N.*) *yoshidai* in Lineage D). It is true that the members of each group are similar to each other in having a large-sized head, small eyes, and long mandibles, but the present result strongly suggests that each species group is not monophyletic and that their macrocephalic forms are convergent.

The evolutionary polarities of the characters inferred from the present analysis indicate that the diagnostic characters of the *sphodroformis* species group (reduction of sexual dimorphism, one seta on antennal segment 2, and a short right paramere of which the apex is rounded) are symplesiomorphies of *Nialoe*. The polyphyly of the *sphodroformis* species group results from its definition by only synplesiomorphies.

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REFERENCES

Allen RT (1980) A review of the subtribe Myadi: description of a new genus and species, phylogenetic relationships, and biogeography (Coleoptera: Carabidae: Pterostichini). Coleopterists Bull 34: 1–29

Berlov O, Plutenko (1997) Two new subgenera of the genus *Pterostichus* (Coleoptera, Carabidae) from the Far East of Russia. Vestnik Irkutskoy Gosudarstvennoy Sel'skokhozyaystevennoy Akademiii 5: 47–51

Bousquet Y (1999) Supraspecific classification of the Nearctic Pterostichini (Coleoptera: Carabidae). Association des Entomologists Amateurs du Québec, Québec

Bousquet Y (2003) Tribe Pterostichini Bonelli, 1810. In "Catalogue of Palaearctic Coleoptera Volume1 Archostemata–Myxophaga–Adephaga" Ed by I Löbl, A Smetana, Apollo Books, Stenstrup, pp 469–520

Bandmayr P, Brandmayr TZ (1994) The evolutionary history of the genus *Abax* (Coleoptera, Carabidae). In "Carabid beetles: ecology and evolution" Ed by K Desender, M Dufrêne, M Loreau, ML Luff, J-P Maelfait, Springer, pp 19–24

Farris JS (1969) A successive approximations approach to character weighting. Syst Zool 18: 374–385

Habu A (1981) Female genitalia of Pterostichini species mainly from Japan (II) (Coleoptera, Carabidae). Ent Rev Jpn 36: 33–53

Ishida H (1958) Some new or little known species of the genus *Pterostichus* Bonelli (Coleoptera, Carabidae) from Japan (I). Ent Rev Jpn 9: 5–8

Jedlička A (1962) Monographie des Tribus Pterostichini aus Ostasien (Pterostichini, Trigonotomi, Myadi) (Coleoptera - Carabidae). Abh Ber Staat Mus Tierk Dresden 26: 177–346

Kasahara S (1988) Distribution pattern and speciation of pterostichine carabid beetles in Japan. In "The beetles of Japan, with special reference to their origin and speciation" Ed by M Satô, Tôkai University Press, Tokyo, pp52–65 [in Japanese]

Kasahara S, Ito Y (1987) A new *Pterostichus* (Coleoptera, Carabidae) from the upper hypogean zone of central Shikoku, southwest Japan. Kontyû 55: 139–145

Koch (1986) Morphological-physiological studies on *Pterostichus* "*nigrita*" (Col., Crab.), a complex of sibling species In "Carabid beetles, their adaptations and dynamics" Ed by PJ den Boer, ML Luff, D Mossakowski, F Weber, Gustav Fischer, New York, pp 269–279

Kryzhanovskij OL, Belousov IA, Kabak II, Kataev BM, Makarov KV, Shilenkov VG (1995) A Checklist of the Ground-Beetles of Russia and Adjacent Lands (Insecta, Coleoptera, Carabidae). Pensoft Publishers, Sofia

Lafer GS, Park JK, Paik JC (2001) A new pterostichine beetle of the subgenus *Nialoe* Tanaka from South Korea (Coleoptera, Carabidae). Insecta Koreana 18: 243–248

Morita S (1992) A new subgenus and species of *Pterostichus* (Coleoptera, Carabidae) from Aomori Prefecture, north Japan. Elytra 20: 15–19

Morita S (1996a) A little known pterostichine carabid, *Pterostichus hozumii* Ishida (Coleoptera, Carabidae). Japanese Journal of Systematic Entomology 2: 133–136

Morita S (1996b) *Pterostichus ohkurai* (Coleoptera, Carabidae), a new relative of *Pterostichus latistylis* from the subalpine zone of the Japanese Alps. Elytra 24: 197–202

Morita S (1998) A new *Pterostichus* (Coleoptera, Carabidae) from the southern Japanese Alps. Elytra 26: 297–302

Morita S (2001) A new *Pterostichus* (Coleoptera) from western Kyushu, west Japan. Japanese Journal of Systematic Entomology 7: 35–39

Morita S (2002) Pterostichine carabid beetles of the subgenus *Cryobius* (Coleoptera, Carabidae) from north Japan. Elytra 30: 73–89

Morita S (2003) Two new *Pterostichus* (Coleoptera, Carabidae) from Honshu, Japan. Japanese Journal of Systematic Entomology 9: 1–8

Morita S, Kanie N (1997) A new macrocephalic pterostichine (Coleoptera, Carabidae) from central Japan. Elytra 25: 163–

167
Nakane T (1979) New or little-known Coleoptera from Japan and adjacent regions, XXX. Reports of the Faculty of Science of Kagoshima University (Earth Science and Biology) 12: 51–60
Nemoto K (1988) *Pterostichus opacipennis* Jedlièka and its allied species of South Korea and Japan (Coleoptera, Carabidae). Bulletin of the Biogeographical Society of Japan 43: 39–45
Nemoto K (1989a) A new species of *Pterostichus* from Amami-Ôshima island, southwest Japan (Coleoptera: Carabidae). Akitu, New series 106: 1–6
Nemoto K (1989b) Systematic position of *Pterostichus yoritomus* Bates and its allied species of Japan (Coleoptera, Carabidae). Bulletin of the Biogeographical Society of Japan 44: 123–125
Park JK, Kwon YJ (1996) A new subgenus *Pterostichus* from Korea (Coleoptera: Harpalidae). Korean Journal of Entomology. 26: 93–103
Park JK, Paik JC (2001) Coleoptera (Carabidae). Economic insects of Korea 12. Insect Koreana Suppl. 19. National Institute of Agricultural Science and Technology, Suwon [in Korean]
Park JK, Kwon YJ, Lafer GS (1996) Classification of the genus *Pterostichus* Bonelli from Korea (Coleoptera: Harpalidae) I. *Micronialoe* subgen. nov. Korean J Entomology 26: 72–77
Sasakawa K (2004) Systematic position of *Pterostichus defossus* Bates, 1883 (Coleoptera, Carabidae). Biogeography 6: 69–73
Sasakawa K (2005a) Taxonomic notes on *Myas* Strum, 1826 (Coleoptera, Carabidae, Pterostichini) of Japan. Biogeography 7: 11–20
Sasakawa K (2005b) *Pterostichus macrogenys* Bates, 1883 (Coleoptera, Carabidae) and its allied species of Northern Japan. Biogeography 7: 69–78
Sasakawa K, Kubota K (2005) Cryptic species of the subgenus *Morphnosoma* Lutshnik (Coleoptera, Carabidae, genus *Pterostichus*) from Japan. Entomol Sci 8: 389–404
Sugimura A (2002) A new subspecies of *Pterostichus todai* Morita et Kanie (Coleoptera, Carabidae) from Mt. Kisokoma-ga-take, Central Japan. Elytra 30: 91–99
Swofford DL (2002) PAUP*. Phylogenetic analysis using parsimony (*and other methods), Version 4. Sinauer Associstes, Sunderland
Tanaka K (1958) A new subgenus and two new species of the genus *Pterostichus* from Japan (Carabidae, Coleoptera). Kontyû 26: 78–83
Tanaka K (1961) Studies on the genus *Pterostichus* from Japan (VII). *spiculifer*-group (Carabidae, Coleoptera). Mushi 35: 39–49
Tanaka K (1985) Pterostichinae. In "The Coleoptera of Japan in Color", Ed by S-I Ueno, Y Kurosawa, M Satô, 2: 104–135, 139 [Plates 20–25]. Hoikusha, Osaka [in Japanese]
Tanaka K, Ishida H (1972) Studies on the genus *Pterostichus* from Japan (VII) (Carabidae, Coleoptera). Ent Rev Jpn 24: 14–16

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Appendix 1. Species and character matrix used in phylogenetic analyses.

Species	Locality of specimens or source	Characters
		1 1 1 1 1 1 1 1
		1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7
Pterostichus (Nialoe) fujimurai Habu	Akawase, Kamisaibara-mura, Okayama [OY]	2 0 3 0 0 1 0 1 0 1 0 2 0 0 2 0 0
P. (N.) mirificus Bates	Mt. Hachimantai, Matsuo-mura, Iwate [KS]	0 0 0 0 0 0 0 1 0 1 0 1 0 0 0 0 1
P. (N.) symmetiricus Straneo	Sasuna, Is. Tsushima, Nagasaki [RI]	0 1 1 1 2 3 3 1 0 1 0 0 0 0 0 2 0
P. (N.) touzalini Andrewes	Mt. Hallasan, Is. Jejudo, Korea [TS]	0 1 0 1 1 3 3 1 0 1 0 1 0 0 0 2 0
P. (N.) yakushimanus Nakane and Ishida	Is. Yakushima, Kagoshima [SS]	0 0 0 1 0 3 4 1 0 1 0 0 0 0 0 2 0
P. (N.) plesiomorphus Nemoto	Is. Amami-ôshima, Kagoshima [JO, KH]	0 0 1 1 1 3 1 1 0 2 0 0 0 0 0 0 0
P. (N.) miyamai Kasahara and Ito	Kashiyama, Tosa-chô, Kôchi [KS]	0 0 0 1 0 0 0 1 0 4 0 0 0 0 0 0 0
P. (N.) macrogenys Bates	Tôbakusawa, Ôtaki-mura, Saitama [TM]	0 0 2 0 0 0 0 1 0 3 1 0 0 0 0 0 0
P. (N.) microps Heyden	Jedlička (1962), Berlov & Plutenko (1997)	0 0 0 0 0 0 0 1 0 3 ? 0 2 0 0 0 0
P. (N.) yoshidai Kasahara	Mt. Kôtsusan, Tokushima [SM]	0 0 0 1 0 0 1 1 0 4 0 0 1 0 0 0 0
P. (N.) teretis Park and Kwon	Park and Kwon (1996)	0 0 0 0 0 0 1 1 0 0 ? 0 ? 0 0 0 0
P. (N.) bellator (Tschitschérine)	Mt. Odaesan, Korea [FZUT]	0 0 0 0 0 0 1 1 0 3 1 0 3 0 0 0 0
P. (N.) opacipennis Jedlička	Sasuna, Is. Tsushima, Nagasaki [RI]	0 0 0 0 0 0 2 1 0 0 1 0 3 0 0 0 0
P. (N.) macrocephalus Habu	Mt. Taradake, Nagasaki [KM, NSMT]	0 0 0 1 0 3 3 1 0 2 0 0 1 0 0 0 0
P. (N.) ishuzuchiensis Kasahara	Mt. Tengunomori, Kôchi [MW]	0 0 0 1 0 0 1 1 0 4 0 0 1 0 0 0 0
P. (N.) abaciformis Straneo	Mt. Tsurugidake, Toyama [KS]	0 1 0 3 2 0 1 1 0 1 0 0 1 0 0 0 0
P. (N.) mucronatus Straneo	Mt. Hakutaisan, Saitama [KS]	0 0 0 3 1 0 1 1 0 1 0 0 1 0 0 1 0
P. (N.) sphodroformis Bates	Mt. Kenashiyama, Okayama [OY]	0 0 0 1 0 0 1 1 0 4 0 0 0 0 0 0 0
P. (N.) pseudopachinus Nakane	Mt. Hiruzen, Okayama [OY]	0 0 0 1 0 0 1 1 0 4 0 0 1 0 0 0 0
P. (N.) mashidai Ishida	Mt. Yamanoriyama, Okayama [OY]	0 0 0 1 0 0 0 1 0 3 0 0 0 0 0 0 0
P. (N.) mosaicus Sasakawa	Is. Fukuejima, Nagasaki [NSMT]	0 1 2 1 0 0 1 1 0 1 0 0 1 0 0 2 0
P. (N.) sincerus Park and Kwon	Mt. Jirisan, Korea [FZUT]	0 0 0 0 0 2 0 1 0 2 0 0 2 0 0 3 0
P. (N.) praedo (Tschitschérine)	Mt. Sobaeksan, Korea [FZUT]	0 0 0 0 0 0 1 1 0 2 0 0 3 0 0 3 0
P. (N.) spiculifer yatsuensis Straneo	Karasawa-Spa, Mts. Yatsu, Nagano [KS]	3 0 2 2 0 2 1 1 0 1 0 0 0 0 2 0 0
P. (N.) dandonis Kasahara	Uratani, Mt. Dantosan, Aichi [KS]	3 0 2 2 0 2 1 1 0 1 0 0 0 0 2 0 0
P. (N.) uenoi Straneo	Mt. Hakutaisan, Saitama [KS]	4 0 0 0 0 2 1 1 0 1 0 1 0 0 1 0 0
P. (N.) omogoensis Nakane	Mt. Ishizuchisan, Ehime [MW]	4 0 3 0 0 2 1 1 0 1 0 1 0 0 3 0 0
P. (N.) latistylis Tanaka	Mt. Hakutaisan, Saitama [KS]	1 0 1 0 0 1 0 1 0 1 0 2 0 0 1 0 0
P. (N.) asymmetricus Bates	Kinshô-Pass, Mts. Nikko, Tochigi [RI]	3 0 0 0 0 1 0 1 0 1 0 2 0 0 3 0 0
P. (N.) katashinensis naganoensis Tanaka	Karasawa-Spa, Mts. Yatsu, Nagano [KS]	3 0 3 0 0 1 0 1 0 1 0 2 0 0 3 0 0
P. (Lianoe) dufouri (Dejean)	"Prov. de Gerona, France" [NSMT]	2 0 0 0 1 2 1 1 2 3 0 0 0 1 0 0 0
P. (Pterostichus s. str.) *cristatus* (Dufour)	no date [NSMT] (Det. S. L. Straneo)	2 0 0 0 1 2 1 1 1 3 0 0 0 1 0 0 0
P. (Myosodus) schonherri Faldermann	"riv. Supsa, Mts. Adjaro-Jmeretian" [NIAES]	4 0 0 0 0 0 0 0 0 3 0 0 0 1 0 0 0
P. (M.) lacunosus roubalianus (Lutshnik)	"Pscbai. Cauc. sept." [NIAES]	4 0 0 0 0 0 0 0 0 3 0 0 0 1 0 0 0

Abbreviations of collectors, providers or depositories (in square brackets): FZUT, Laboratory of Forest Zoology, Department of Forest Science, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan; HK, H. Karube; JO, J. Ogawa; KM, K. Matsumoto; KS, K. Sasakawa; MW, M. Wakabayashi; NIAES, National Institute for Agro-Environmental Sciences, Tsukuba, Japan; NSMT, The National Science Museum, Tokyo, Japan; OY, O. Yamaji; RI, R. Ishikawa; SM, S. Mano; SS, S. Shiokawa; TM, T. Maehara; TS, T. Sota.

Appendix 2. Character evaluation and coding. All characters were treated as unordered.

1. Right paramere: short and almost rounded apically (0); spatulate and hardly bent in ventral direction (1); spatulate and distinctly bent in ventral direction (2); moderately long and pointed apically (3); elongated (4).
2. Right pigmented band: absent (0); more or less present (1).
3. Left pigmented band: absent (0); present, but rudimentary to weak (1); present and distinctly sclerotized, but not connected with sclerotized part of aedeagus (2); present and connected with sclerotized part of aedeagus (3).
4. Basal sclerite: absent (0); present without conspicuous ridge (1); raised in plate (2); well developed (3).
5. Median pigmented lobe: absent (0); small (1); strongly lobate with distinct sclerotization (2).
6. Shape of left preapical lobe: small to equal to other lobes on the left lateral side of endophallus (0); larger than other lobes on the left ventral side of endophallus (1); developed but weakly lobate, without other lobes on the left ventral side of endophallus (2); strongly lobate without other lobes on the left ventral side of endophallus (3).
7. Dorsal surface of left preapical lobe: not sclerotized (0); weakly sclerotized (1); weakly sclerotized with distictly sclerotized projection (2); strongly sclerotized (3); strongly sclerotized with distictly sclerotized projection (4).
8. Gonoporal piece: absent (0); present (1).
9. Apical sclerite: absent or rudimentary (0); sclerotized and weakly swollen (1); sclerotized and strongly lobate (2).
10. Shape of endophallus: short and straight (0); short and weakly bent in left lateral to ventrolateral direction (1); short and strongly bent toward ventral side of aedeagus (2); long and strongly bent toward ventral side of aedeagus (3); long and strongly bent toward right ventrolateral to lateral direction (4).
11. Pigmentation on innermost part of ventral side: absent (0); present (1).
12. Setae on antennal segment 2: one seta (0); two setae (1); more than three setae (2).
13. Dorsal surface of pronotum and elytra: shiny (0); shiny except for female elytra, which are opaque (1); opaque except for pronotum, which is varied from shiny to opaque at the individual level (2); opaque (3).
14. Setae on ventral side of last tarsal segment: absent (0); present (1).
15. Resection of male sternum 7: never truncate (0); slightly truncate (1); distinctly and almost symmetrically truncate (2); distinctly and asymmetrically truncate (3).
16. Median projection on male sternum 7 (except for *P.* (*N.*) *mirificus*): absent (0); rudimentary (1); distinct but barely bent toward ventral side (2); broad and distinctly bent toward ventral side (2).
17. Bufricated projection on male sternum 6 : absent (0); present (1)